The Wilson Journal of Ornithology 119(3):400–409, 2007

CHANGES IN BIRD COMMUNITIES AND WILLOW HABITATS ASSOCIATED WITH FED ELK

ERIC M. ANDERSON[1,2]

ABSTRACT.—I assessed changes in bird distributions associated with alteration of riparian willow (*Salix* spp.) habitat by supplementally-fed elk (*Cervus elaphus nelsoni*) in western Wyoming, USA. Bird communities in stands close to (n = 4) and distant from (n = 4) feeding stations were dissimilar (complement of the Morisita-Horn index = 0.27). Stands close to feeding stations had lower species richness and relative abundances of all birds while relative abundances of all shrub-steppe species were greater, an effect of elk-induced conversion of willow to shrub-steppe habitat. Elk affected habitat mainly by reducing willow cover <2 m in height. Reductions in willow cover at >0.5–1 and >1–2 m, relative to 11 alternative variables, were responsible for declines in Willow Flycatchers (*Empidonax traillii*), MacGillivray's Warblers (*Oporornis tolmiei*), and Fox Sparrows (*Passerella iliaca*). Elk feeding in the Gros Ventre River Valley had reduced but similar effects on birds and habitat despite a smaller number of elk fed (1,900 vs. 9,200 annually for 1994–1998) and a shorter duration of feeding (initiation in 1960 vs. 1912) relative to the National Elk Refuge. These effects can extend at least 1.5 km.
Received 29 June 2006. Accepted 11 November 2006.

Supplemental feeding that began in 1912 has contributed to elevated densities of elk (*Cervus elaphus nelsoni*) in winter on the National Elk Refuge (NER) (Smith 2001). Both public and private feeding programs for wild ungulates have since become common (Smith 2001; EMA, unpubl. data). Habitat alteration by elk has been reported on the NER (Murie 1951, Craighead 1952, Smith et al. 2004) and is a typical consequence of high densities of native ungulates generally (Alverson et al. 1988, Brandner et al. 1990, Teer 1997). Several reports suggest that browsing by elk is the most important proximate cause of degradation and loss of willow (*Salix* spp.) habitat in Yellowstone National Park (Singer et al. 1998), where elk were fed until the 1920s, and Rocky Mountain National Park (Hess 1993).

Past studies indicate that birds are particularly sensitive to degradation of riparian areas by domestic ungulates (e.g., Saab et al. 1995, Tewksbury et al. 2002). Browsing of shrubs and trees by locally abundant wild ungulates can reduce bird abundance, diversity, and productivity (Braun et al. 1991, McShea et al. 1995, Berger et al. 2001). However, effects on birds related to feeding programs that increase densities of wild ungulates have received little critical evaluation (but see Dobkin et al. 2002).

Some bird species decline due to browsing by domestic ungulates (e.g., Willow Flycatcher [species names in Table 1]; Sedgwick 2000), but many other common species display variable responses (e.g., Yellow Warbler, Song Sparrow; Saab et al. [1995] present lists of species). The magnitude of declines in the former group and the direction of change in the latter group likely vary due to differences in variables such as ungulate density, duration and seasonal timing of use, and habitat type (Fleischner 1994, Saab et al. 1995, Tewksbury et al. 2002). The greater densities and longer durations of elk use on the NER have likely increased impacts to habitat and birds relative to most studies of domestic ungulates. Conversely, the different seasonal timing of use on the NER (i.e., winter vs. non-winter) may have moderated these effects because vegetation is dormant and at times protected by snow (Smith 2001).

My objectives were to: (1) examine whether willow structure explained bird distributions, and (2) describe how elk feeding operations affected willow structure.

METHODS

Study Area.—Study sites were on federal land in the Jackson Hole and Gros Ventre River valleys in Teton County, Wyoming, USA

[1] Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Department 3166, 1000 E. University Ave., Laramie, WY 82071, USA.

[2] Current address: Department of Zoology and Physiology, University of Wyoming, Department 3166, 1000 E. University Ave., Laramie, WY 82071, USA; e-mail: emander@uwyo.edu

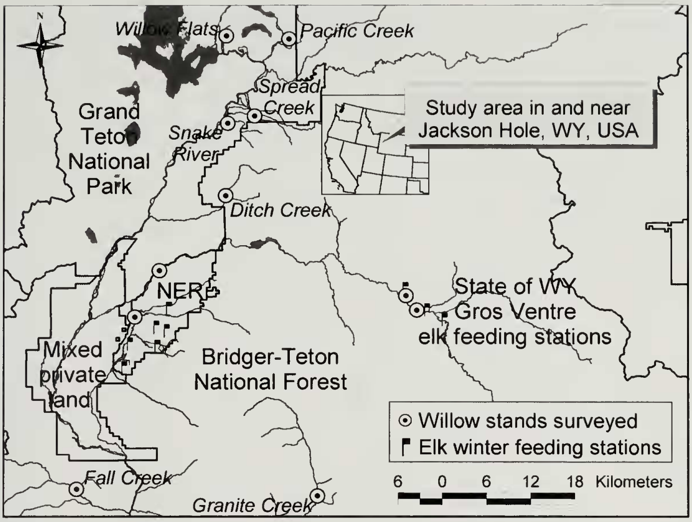

FIG. 1. Study area and sites in Teton County, Wyoming, USA. Snake River, Spread Creek, and Willow Flats were the three additional stands used in bird-habitat models.

(Fig. 1). Elevations near the southern end of Jackson Hole and the east end of the Gros Ventre River Valley are approximately 1,800 and 2,250 m, respectively. Mean temperature, precipitation, and snowfall are 14.7° C, 9.8 cm, and 0.3 cm respectively during summer (Jun–Aug), and −7.8° C, 10.2 cm, and 128.0 cm, respectively, during winter (Dec–Feb; 1948–2006; Jackson, Wyoming, Western Regional Climate Center).

I considered willow sites associated with both federal (NER) and state (Wyoming Game and Fish Department) supplemental feeding programs. The NER is administered by the U.S. Fish and Wildlife Service and has operated winter supplemental feeding stations for elk all but nine winters since inception in 1912 (Smith et al. 2004). State feeding stations considered (Alkali Creek, Fish Creek, and Patrol Cabin) are in the Gros Ventre River Valley of the Bridger-Teton National Forest. State (referred to as Gros Ventre) feeding stations were operated only during severe winters prior to 1956 and have operated nearly every year since 1960 (Boyce 1989). The approximate average number of elk fed for the years 1994–1998 was 9,200 for the NER and 1,900 for the three Gros Ventre sites combined (Smith 2001).

Study Design.—I reduced the influence of factors other than elk on habitat and birds by selecting willow stands with the following criteria: (1) dominance by tall willow species (i.e., those typically attaining heights >2 m), (2) adjacent habitat mainly shrub-steppe dominated by sagebrush (*Artemisia* spp.), (3) mean slope less than 4°, and (4) little use in the past ~50 years by domestic ungulates or moose (*Alces alces*; as verified by reports and observations of federal and state biologists).

Ungulate density at the stand scale has been used to infer effects of wild ungulates on habitat and birds (DeCalesta 1994), but is not available for my study area. I used two alternative techniques to evaluate effects of fed elk. First, I compared bird communities, elk use, and habitat structure between stands close (<5 km) to feeding stations (two stands in the NER and two stands adjacent to Gros Ventre feeding stations) and stands distant (16–36 km) from feeding stations (Ditch Creek, Fall Creek, Granite Creek, Pacific Creek; Fig. 1). The locations of NER and Gros Ventre feeding stations have changed little over time (Smith 2001). Thus, proximity to these stations should be an appropriate metric of long-term effects of elk feeding on habitat. Habitat alteration by moose in this area occurs primarily in Grand Teton National Park (Berger et al. 2001); only the Pacific Creek stand is in this park and the area I considered had little evidence (fecal pellets, tracks) of moose pres-

TABLE 1. Habitat and bird comparisons between willow stands close to (n = 4) and distant from (n = 4) elk feeding stations. All bird data are for mean detections per 35-m survey point.

	Mean (SE)		
	Stands close	Stands distant	$F_{1,6}$ (P)
Elk use measures			
Willow annual segments browsed (%)	88.2 (7.1)	28.5 (5.9)	41.71 (<0.001)
Willow <0.6 m tall browsed (%)	95.8 (4.3)	55.0 (11.7)	10.67 (0.017)
Habitat measures			
Willow height (m)	1.4 (0.4)	1.9 (0.3)	1.24 (0.31)
Grass cover (%)	64.9 (6.1)	27.1 (6.8)	17.17 (0.006)
Forb cover (%)	11.1 (2.1)	15.8 (5.0)	0.77 (0.41)
Bare ground cover (%)	2.1 (1.0)	5.9 (0.7)	10.33 (0.018)
Stagnant water cover (%)	0.5 (0.4)	1.0 (0.5)	0.49 (0.51)
Flowing water cover (%)	0.4 (0.4)	1.1 (0.4)	1.47 (0.27)
Bird community measures			
Total relative abundance	8.5 (1.8)	14.6 (1.4)	7.39 (0.035)
Species richness	5.7 (1.0)	8.7 (0.2)	8.19 (0.029)
Shrub-steppe bird relative abundance[a]	2.4 (0.5)	0.1 (0.03)	23.93 (0.003)
Bird species relative abundance[b]			Proximity effect (95% CI)[c]
Calliope Hummingbird (*Stellula calliope*)	0.0 (0.0)	0.7 (0.4)	−1.2 (−2.7, 0.3)
Willow Flycatcher (*Empidonax traillii*)	0.1 (0.1)	0.8 (0.3)	−1.7 (−3.3, −0.1)
Dusky Flycatcher (*E. oberholseri*)	0.2 (0.1)	0.6 (0.3)	−1.0 (−2.5, 0.5)
American Robin (*Turdus migratorius*)	0.2 (0.1)	0.2 (0.1)	−0.1 (−1.5, 1.3)
Gray Catbird (*Dumetella carolinensis*)	0.0 (0.0)	0.3 (0.1)	−1.3 (−2.9, 0.2)
Yellow Warbler (*Dendroica petechia*)	1.5 (0.5)	2.9 (0.4)	−1.3 (−2.9, 0.2)
MacGillivray's Warbler (*Oporornis tolmiei*)	0.03 (0.03)	1.5 (0.5)	−1.9 (−3.5, −0.2)
Common Yellowthroat (*Geothlypis trichas*)	0.4 (0.3)	1.1 (0.7)	−0.6 (−2.0, 0.9)
Fox Sparrow (*Passerella iliaca*)	0.1 (0.1)	1.0 (0.3)	−1.8 (−3.5, −0.2)
Savannah Sparrow (*Passerculus sandwichensis*)	0.9 (0.4)	0.0 (0.0)	1.4 (−0.2, 2.9)
Lincoln's Sparrow (*Melospiza lincolnii*)	1.5 (0.8)	0.9 (0.5)	0.4 (−1.0, 1.8)
Song Sparrow (*M. melodia*)	1.0 (0.4)	2.2 (0.5)	−1.3 (−2.8, 0.3)
Vesper Sparrow (*Pooecetes gramineus*)	0.3 (0.3)	0.0 (0.0)	0.6 (−0.8, 2.0)
White-crowned Sparrow (*Zonotrichia leucophrys*)	0.3 (0.1)	0.4 (0.3)	−0.4 (−1.8, 1.0)
Brewer's Blackbird (*Euphagus cyanocephalus*)	0.7 (0.7)	0.0 (0.0)	0.7 (−0.8, 2.1)
Brown-headed Cowbird (*Molothrus ater*)	0.4 (0.1)	0.7 (0.2)	−1.0 (−2.4, 0.5)

[a] Shrub-steppe birds include: Brewer's Sparrow (*Spizella breweri*), Savannah Sparrow, Vesper Sparrow, Bobolink (*Dolichonyx oryzivorus*), Western Meadowlark (*Sturnella neglecta*), Red-winged Blackbird (*Agelaius phoeniceus*), and Brewer's Blackbird.

[b] Bird species detected rarely (i.e., more than a single observation for each group of stands, yet mean detections <0.2) followed by proximity effects (with 95% CI) include: Wilson's Warbler (*Wilsonia pusilla*) 0.8 (−0.7, 2.2), Brewer's Sparrow 0.6 (−0.9, 2.0), Bobolink 0.6 (−0.8, 2.0), Western Meadowlark 0.6 (−0.8, 2.0), and Red-winged Blackbird 1.1 (−0.4, 2.5).

[c] Proximity effects are changes in species abundance related to proximity to elk feeding stations (i.e., stands close to and distant from elk feeding stations are the treatment and control groups, respectively).

ence. Granite Creek is a tributary of the Hoback River (a tributary of the Snake River). All other stands are on tributaries of the Snake River and are dominated by *Salix boothii* and *S. geyeriana*. The approximate densities of willow species that rarely attain 2 m in height (*S. wolfii*, *S. lemmonii*, and *S. planifolia*) are lower and similar among all stands except Granite Creek, which is dominated by *S. wolfii* and *S. boothii*. The greater presence of *S. wolfii* on Granite Creek may bias downwards my estimates of elk effects on willow height and cover >1 m. All *Salix* specimens were identified by R. D. Dorn following Dorn (2001).

I modeled relationships between elk use (i.e., browse rate) and habitat structure, and between habitat structure and bird abundance as a second test of elk-feeding effects. Browse rate was the percentage of annual segments browsed excluding the current year's growth on willow stems >1 cm in diameter (described further in *Habitat Surveys*). I interpreted a significant relationship between browse rate and a habitat variable across the above eight willow stands to suggest influence of elk on the habitat variable.

I used a two-step approach to evaluate the influence of elk feeding on individual bird species. First, I considered effect sizes on species abundance due to proximity to elk feeding stations (i.e., stands close to and distant from elk feeding stations constitute the treatment and control groups, respectively). Second, I developed habitat models for the four species with the greatest and four species with the smallest absolute effect sizes to evaluate the likelihood that elk have influenced effect sizes. Variation in the abundance of species with large effect sizes (species predicted to be more sensitive to elk use) should be explained by habitat variables influenced by elk. Conversely, species with small effect sizes (species predicted to be less sensitive to elk use) should be related to habitat variables over which elk have little influence or that were not controlled for during stand selection. I included in these models three additional stands in Grand Teton National Park (Fig. 1). Moose may have altered willow structure in these three stands, but their inclusion in the habitat models seems acceptable because I was interested in the relationship between bird distributions and habitat variables.

I tested for differences in browse rate, and in bird and habitat variables between the NER and Gros Ventre feeding areas to examine the importance of feeding characteristics (i.e., number of elk, years since feeding began). I also considered the relationship between browse rate and distance to the nearest feeding station to examine the spatial extent of feeding effects.

Bird Surveys.—I used 35-m radius point counts for bird surveys (Ralph et al. 1995). Each count lasted 20 min and each point was visited on three occasions in 2001 (19 May–4 Jul) over which species detections were averaged. I randomly located five points in each stand (the maximum number possible provided the smallest willow stand area) over which all bird measures were averaged. I continuously mapped locations of birds to avoid counting individuals more than once. Shrub-steppe birds were those species that nest in grassland and low shrub habitat, as well as species that typically nest in riparian habitat lacking significant willow structure (Table 1). Red-winged Blackbirds nest in willow as well as in non-woody emergent vegetation. Brewer's Blackbirds nest in willow and non-riparian shrubs. Both blackbird species were included in the shrub-steppe guild because they were observed almost exclusively within survey plots lacking substantial willow structure (Anderson 2002). I used the Morisita-Horn index (Dobkin et al. 1998) to measure community similarity between stands close to and distant from feeding stations. The complement of this index ranges from 0 (no similarity) to 1 (complete similarity).

Habitat Surveys.—All habitat variables were measured from 12 standardized locations within each 35-m radius bird survey point. I measured the distance to the center of the nearest willow shrub and its maximum height at each location, and used the point-centered quarter method to estimate stand density of willow shrubs (Bonham 1989). I recorded foliage volume at each location using the stacked cube method (Kus 1998). This involved recording percent cover for willow and for a class of other shrubs (almost exclusively shrubby cinquefoil [*Dasiphora floribunda*]) within a 1-m^2 sampling column at 0–0.5, >0.5–1, >1–2, and >2 m height classes. I also recorded within these 1-m^2 plots: cover <0.5 m of grasses, forbs, bare ground, stagnant water, and flowing water. Cover classes were: <1, >1–10, >10–25, >25–50, >50–75, >75–90, and >90%.

I documented two measures of browse use from each of the 12 locations. First, I located on the nearest willow shrub the northern-most and southern-most stems with diameter >1 cm and height 0.5–2 m (the approximate height range available in winter to browsing wild ungulates; Keigley and Frisina 1998). I then recorded browse rate on each of these two stems by cover classes. Second, if the closest willow was <0.6 m in height, I recorded only whether it had been browsed. These measures were strongly correlated (R = 0.82, P = 0.013). Thus, only browse rate was used as a metric of elk use of each willow stand.

Statistical Analyses.—I conducted statistical analyses using JMP 5.0.1 (SAS Institute Inc. 2002). I used one-way analysis of variance

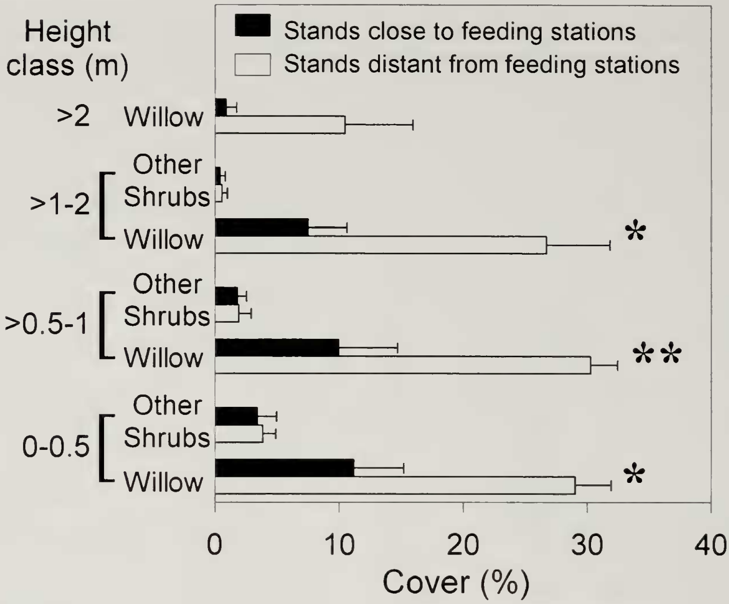

FIG. 2. Mean (+SE) cover of willow and other shrubs at multiple heights in stands close to (n = 4) and distant from (n = 4) elk feeding stations. Other shrubs were absent above 2 m (*$P < 0.05$; **$P < 0.01$).

(ANOVA) to test for differences between two means and Duncan's Multiple Range Test for pairwise comparisons among three means. I used the Welch-Satterthwaite degrees of freedom modification when variances were not homogeneous (Johnson 1995). Levene's Test was used to evaluate variance homogeneity. I used unbiased corrections to estimate effect sizes for bird species based on pooled standard deviations (Hedges and Olkin 1985). I used simple linear regression to test relationships between browse rate and habitat variables. Tests were considered significant when $P < 0.05$.

I used forward stepwise regression (considered appropriate for exploratory purposes; Hosmer and Lemeshow 1989) to model bird associations with habitat variables across all stands (n = 11). I began model development for each species by considering all univariate habitat models. Variables significant at $P <$ 0.25 were retained for further model development (Hosmer and Lemeshow 1989). I then constructed correlation matrices to detect multi-collinearity. I retained the variable that was most biologically relevant or had the lowest P-value in univariate analyses (when biological relevance was not clear) for each pair of strongly correlated ($R > 0.60$) variables. All remaining variables were included in the forward stepwise procedure. Criteria for entry and removal were $P = 0.25$ and $P = 0.10$, respectively.

RESULTS

Stands close to elk feeding stations had a higher mean browse rate and a higher mean percentage of browsed shrubs <0.6 m in height (Table 1). Mean willow cover was lower in stands close to feeding stations for the height classes 0–0.5 ($F_{1,6}$ = 12.93, P = 0.011), >0.5–1 ($F_{1,6}$ = 15.18, P = 0.008), and >1–2 m ($F_{1,6}$ = 10.33, P = 0.018), and non-significantly lower for the height class >2 m ($F_{1,3.1}$ = 2.99, P = 0.18; Fig. 2). Willow shrub height (Table 1) and cover at all height classes for non-willow shrubs (Fig. 2) did not differ among groups of stands. Grass cover was greater and bare ground lower in stands close to feeding stations, while cover of forbs, stagnant water, and flowing water did not differ between groups (Table 1). Elevation ($\bar{x}$ ± SE) did not differ between groups of stands (close 2,100 ± 85 m; distant 2,061 ± 52 m; $F_{1,6}$ = 0.15, P = 0.71), nor was it related to browse rate (R = 0.30, P = 0.47).

I observed 1,743 individual birds within 35-m radius survey points. Total relative

TABLE 2. Regressions of mean habitat variables on browse rate across willow stands (n = 8).

Response variables (stand means)	Coefficient (SE)	r^2	$F_{1,6}$ (P)
Willow density (per ha)[a]	−0.26 (0.52)	0.04	0.25 (0.64)
Willow height (m)	−0.01 (0.01)	0.35	3.20 (0.12)
Willow cover 0–0.5 m (%)	−0.28 (0.08)	0.69	13.14 (0.011)
Willow cover >0.5–1 m (%)	−0.30 (0.09)	0.65	11.39 (0.015)
Willow cover >1–2 m (%)	−0.28 (0.10)	0.55	7.19 (0.036)
Willow cover >2 m (%)	−0.15 (0.09)	0.32	2.84 (0.14)
Other shrub cover 0–0.5 m (%)	0.001 (0.03)	<0.01	<0.01 (0.97)
Other shrub cover >0.5–1 m (%)	−0.0002 (0.02)	<0.01	<0.01 (0.99)

[a] Relationship improved by removal of one observation (r^2 = 0.70, $F_{1,5}$ = 11.41, P = 0.020).

abundance and species richness were lower and relative abundance of shrub-steppe species was greater in stands close to feeding stations (Table 1). The complement of the Morisita-Horn index was low (0.27) indicating little similarity in bird communities between groups of stands.

Increased proximity to elk feeding stations had a negative effect on the relative abundance of most willow-associated species; for Willow Flycatchers, MacGillivray's Warblers, and Fox Sparrows these negative effects were significant (i.e., 95% confidence intervals for effect sizes do not overlap zero; Table 1). Calliope Hummingbirds and Gray Catbirds were not recorded in stands close to feeding stations. Increased proximity to feeding stations had a positive effect on the relative abundance of all shrub-steppe species. None of these positive effects was significant, but all shrub-steppe species except Brewer's Sparrows were observed exclusively within stands close to feeding stations.

Browse rate was unrelated to willow height, willow cover >2 m, and cover of non-willow shrubs across stands (Table 2). Browse rate was negatively related to willow density when a single observation was removed. Browse rate was also negatively related to willow cover for 0–0.5, >0.5–1, and >1–2 m height classes. Models best explaining abundance of four species (Table 3) predicted to be more sensitive to elk use included mainly willow cover at 0–0.5, >0.5–1, and >1–2 m height classes. Only abundances of Common Yellowthroats and White-crowned Sparrows, of the four species predicted to be less sensitive to elk use, were modeled best using habitat variables cor-

TABLE 3. Models of bird species[a] abundance with habitat variables[b] across all stands (n = 11). Forward stepwise regression was used to develop a model for each species from a reduced set of habitat variables.

	Models[c]	r^2	F (P)
Species predicted to be more sensitive to elk use[a]			
Willow Flycatcher	Willow3 (2.27*)	0.36	5.17 (0.049)
MacGillivray's Warbler	Willow2 (3.77**) Other1 (2.08)	0.70	9.45 (0.008)
Fox Sparrow	Willow3 (4.36**)	0.68	18.97 (0.002)
Savannah Sparrow	Willow1 (−2.05)	0.32	4.21 (0.071)
Species predicted to be less sensitive to elk use[a]			
American Robin	Height (2.64*) Elevation (−1.48)	0.54	4.79 (0.043)
Common Yellowthroat	Willow1 (2.09)	0.33	4.37 (0.066)
Lincoln's Sparrow	Other2 (−5.15***) Elevation (4.59**)	0.88	28.51 (<0.001)
White-crowned Sparrow	Elevation (4.86**) Other2 (2.79*) Willow3 (2.24)	0.87	15.08 (0.002)

[a] Species predicted to be more and less sensitive to elk use are those with the largest and smallest absolute effect sizes on abundance due to proximity to elk feeding stations.
[b] Habitat variables considered include: Willow1, 2, 3, 4 (mean % willow cover at 0–0.5, >0.5–1, >1–2, and >2 m height classes, respectively); Other1, 2 (mean % non-willow shrub cover at 0–0.5 and >0.5–1 m height classes, respectively; non-willow shrub cover was usually absent above 1 m); Density (mean for willow shrubs [per ha]); Height (mean for willow shrubs [m]); Grass, Bare ground, Stagnant water, Flowing water (mean % cover <0.5 m); Elevation (m).
[c] Variables included in each model are presented with the t-statistic comparing model performance with and without the variable (* P < 0.05; ** P < 0.01; *** P < 0.001).

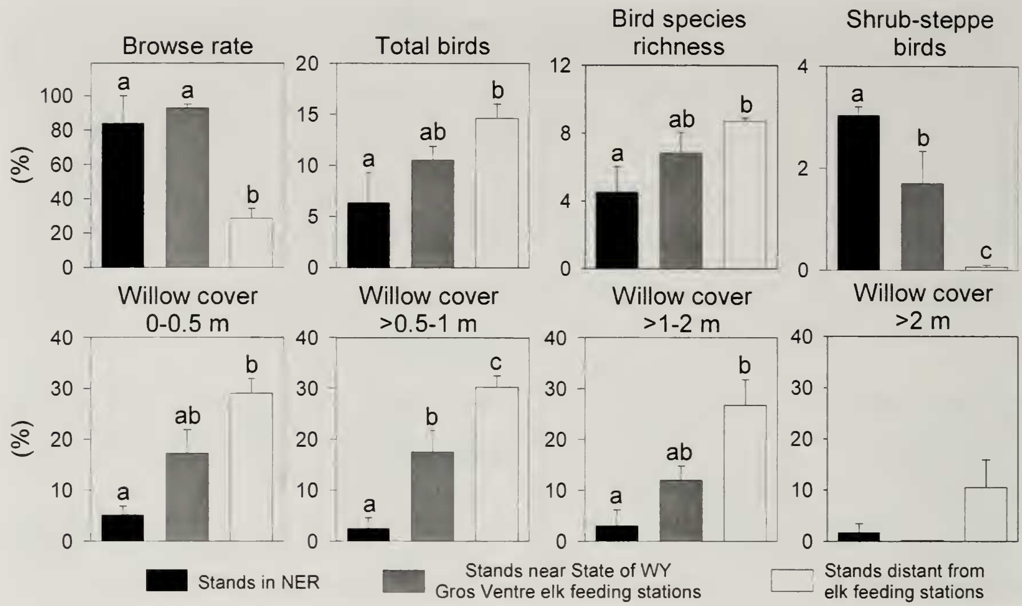

FIG. 3. Mean browse rate, bird, and habitat variables (+SE) in willow stands in the National Elk Refuge (n = 2), stands near State of Wyoming Gros Ventre elk feeding stations (n = 2), and stands distant from elk feeding stations (n = 4). All bird data are for mean detections per 35-m survey point. Different letters denote different groupings ($P < 0.05$).

related with browse rate. Models for these two species, however, did not perform significantly better due to inclusion of habitat variables correlated with browse rate.

NER and Gros Ventre stands had similar browse rates. However, Gros Ventre stands were consistently intermediate to stands distant from feeding stations and NER stands in bird community variables and in willow cover (Figs. 3, 4).

DISCUSSION

Elk reduced willow structure near feeding stations, which promoted reductions in the combined relative abundance of all bird species and increases in all shrub-steppe species. Experimental data on the NER (i.e., ungulate exclosures) indicate a causal relationship between elk feeding and reductions in willow structure (Smith et al. 2004). Historical observations on the NER indicate that impacts to habitat are the result of aggregating elk through supplemental feeding as opposed to normal use of historical winter range of high quality (Preble 1911, Murie 1951, Craighead 1952).

The most prominent effect of elk on habitat was to reduce willow cover <2 m in height. Domestic ungulates induce similar changes to the horizontal structure of willow (Knopf et al. 1988). Sensitivity to browsing by livestock has been documented in three species that appear to be particularly sensitive to habitat alteration by elk: Willow Flycatchers (Sedgwick 2000), MacGillivray's Warblers, and Fox Sparrows (Saab et al. 1995, Tewksbury et al. 2002).

Birds least sensitive to elk use were either habitat generalists (American Robin) or nest mainly on or near the ground: Common Yellowthroat (Guzy and Ritchison 1999), White-crowned Sparrow (Chilton et al. 1995), and Lincoln's Sparrow (Ammon 1995). Declines in species nesting on or near the ground often follow livestock grazing (Saab et al. 1995). Such declines may not be prominent in this case because elk use these willow stands in winter when snow often protects low vegetation (Smith 2001). My results indicate elk reduced mean willow cover <0.5 m in height. Thus, if snow does protect willow it is likely either uncommon or occurs at a lower height range. MacGillivray's Warblers and Fox Sparrows nest in shrubs and on the ground sug-

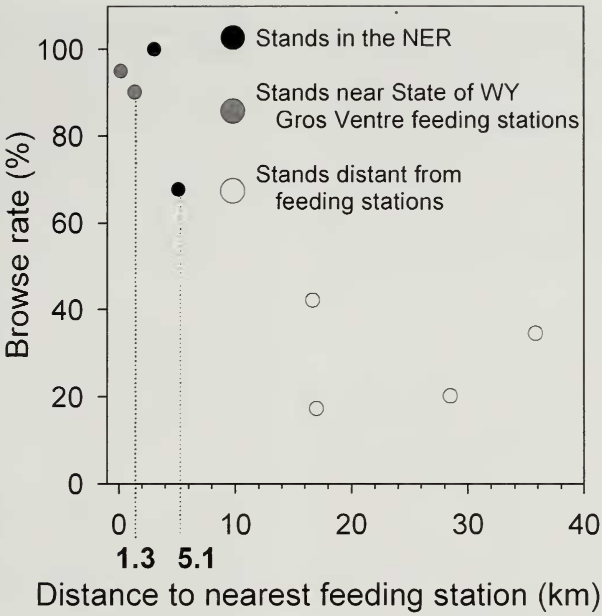

FIG. 4. Relationship of mean browse rate with distance to the nearest elk feeding station. Browse rate was highly correlated with willow cover <2 m and is used as an index of ecological effects of elk feeding.

gesting factors in addition to available nesting habitat may influence sensitivity to elk browsing. For instance, Fox Sparrows forage on the ground under dense cover (Weckstein et al. 2002). The small number of willow stands sampled and consideration of a single breeding season likely contributed to the small effect sizes and limit the resolution of the habitat models.

The willow structure and bird communities near the Gros Ventre feeding stations suggest effects of browsing (Fig. 3) despite a much smaller number of elk fed relative to the NER (1,900 vs. 9,200 annually for 1994–1998). The similar browse rates in these feeding areas despite a shorter duration of feeding in the Gros Ventre (initiation in 1960 vs. 1912) suggest bird and habitat changes could equal or exceed those in the NER. This finding may be the result of greater proximity of Gros Ventre stands to feeding stations (Fig. 4). Evidence from Gros Ventre stands indicates 1.3 km is not sufficient to reduce browse rates and effects on habitat and birds (Figs. 3, 4). The >5 km needed to reduce browse rates in the NER may not be applicable to most feeding programs given the scale of NER feeding.

The NER South stand indicates the potential extent of habitat alteration following a long duration of feeding and close proximity (<3 km) to feeding stations; tall willow structure is nearly absent. The persistence of willow sprouts or seedlings, presence of tall willow "skeletons" and stumps, abundance of tall willow in elk exclosures, and historical photos all indicate a tall willow community previously existed in this area (Smith et al. 2004). The high browse rates in this stand suggest elk eliminated willow structure by preventing replacement of tall willow shrubs.

Several factors increase the relevance of my findings. First, abundant yet non-fed populations of elk in the Intermountain West have likely produced similar changes in bird communities (e.g., Hess 1993, Singer et al. 1994). Second, MacGillivray's Warblers appear highly sensitive to elk use and, unlike most western riparian birds, are neither distributed continent-wide nor are they an eastern species with a range extension (Knopf 1986); long-term surveys of this species may be a critical component of monitoring feeding effects. Third, willow and aspen (*Populus tremuloides*) support greater diversity of flora and fauna than most habitats in this region. Thus, feeding-induced impacts to willow and aspen

(Anderson 2002) may reduce diversity at the landscape scale. Finally, wild ungulate feeding is common (Smith 2001, Peek et al. 2002) and even small, private feeding programs likely affect habitat and birds. Wild ungulates continue to browse vegetation when supplemental feed is available (Schmitz 1990) and can have dramatic effects on habitat at densities as low as four animals per km^2 (Alverson et al. 1988).

ACKNOWLEDGMENTS

I thank S. H. Anderson for guidance and B. L. Smith for conceiving and advocating this project. The U.S. Fish and Wildlife Service and the Wyoming Cooperative Fish and Wildlife Research Unit provided funding. B. L. Smith, Steve Kilpatrick, S. L. Cain, J. D. Ozenberger, and staffs of the NER, Wyoming Game and Fish Department, Grand Teton National Park, and the Bridger-Teton National Forest provided technical and logistical assistance. M. G. Greenlee and M. H. Anderson provided excellent field assistance. Shay Howlin and C. S. Nations assisted with statistical analyses. R. D. Dorn identified willow specimens. W. L. Baker, C. E. Braun, S. W. Buskirk, E. K. Cole, D. S. Dobkin, F. L. Knopf, J. R. Lovvorn, B. L. Smith, and two anonymous reviewers suggested improvements to earlier drafts of this manuscript.

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